

# A new species of *Pteralopex* Thomas, 1888 (Chiroptera : Pteropodidae) from the Fiji Islands

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## Synopsis

The unusual megachiropteran genus *Pteralopex* is briefly reviewed and considered to include three species, two named many years ago from the Solomon Islands, and a third, here described as new, from the Fiji Islands, whence the genus is recorded for the first time. Cuspitation of the molariform teeth in *Pteralopex* is considered in detail, with especial reference to the new species, and compared with the similarly cuspidate condition of the molariform teeth of *Harpyionycteris*. Presumed homologies with the cusps of the dilambdodont teeth of the Microchiroptera are examined, with a discussion of the relevance of molariform cuspitation in the Megachiroptera to theories of their dental evolution.

## Introduction

The known megachiropteran fauna of the Fiji Islands has been limited hitherto to two species of the widespread genus *Pteropus*, one the Pacific fruit bat *P. samoensis*, the other the Polynesian fruit bat *P. tonganus*, and to the long-tailed fruit bat *Notopterus macdonaldi*. None is endemic: *P. samoensis* is represented on the Fiji Islands by an endemic subspecies, *P. s. nawaiensis*, the other, nominate subspecies occurring in the Samoa Islands (Wodzicki & Felten, 1975), while *P. tonganus* is more widely distributed, its subspecies occurring variously from Dampier (Karkar) Island, off the northeastern coast of New Guinea and from Rennell Island, in the Solomon Islands, eastward to the Tonga and Samoa Islands and to Niue Island. This species may occur or have occurred even further to the east, in the Cook Islands, whence bats, apparently pteropodids, have been reported (Smith, 1902, Krzanowski, 1977 : 271) from Raratonga Island (21° 14' S, 159° 46' W) and where there is evidence of bats (Gill, 1876, Krzanowski, 1977 : 271) on Mangaia Island (21° 55' S, 157° 55' W). The subspecies of *P. tonganus* on the Fiji Islands, *P. t. tonganus*, occurs also in the Tonga and Samoa groups to the east, but to the west is replaced by *P. t. geddiei* on the Loyalty Islands, New Caledonia and the New Hebrides. The representatives of *Pteropus* on the Fiji Islands thus display a closer affinity to those of the more easterly islands than to their congeners on the islands to the west of the Fiji group. *Notopterus macdonaldi* has a rather different distributional pattern: one subspecies, *N. m. macdonaldi*, occurs on the Fiji Islands and in the New Hebrides (specimens reported from Ponape, Caroline Islands by Jentink (1887 : 268, 1888 : 158) are referred to this subspecies by Andersen (1912 : 798) who also (p. lxxiv) queries

the veracity of the record) with a second subspecies, *N. m. neocaledonica*, in New Caledonia. The microchiropteran fauna of the Fiji Islands is similarly sparse with records only of *Emballonura semicaudata* and *Tadarida jobensis*. As among the Megachiroptera there is no endemic species: *E. s. semicaudata* occurs also in the Tonga and Samoa groups and in the New Hebrides, with a second subspecies in the Palau Islands, while the distribution of *T. jobensis* extends from the Fiji Islands to New Guinea and Australia. Specimens of the latter species from the Fiji Islands seem likely to represent *T. j. bregullae*, described originally from the New Hebrides (Felten, 1964a : 12).

The islands to the east of the Fiji group have fewer species, with *Pteropus tonganus* and *Emballonura semicaudata* in the Tonga Islands, occurring together with *Pteropus samoensis* in the Samoa Islands. To the west of Fiji, however, the islands and island groups have a more diverse bat fauna. Apart from *Notopterus macdonaldi* on New Caledonia and the New Hebrides, the Megachiroptera are represented by several species of *Pteropus*, all except *P. tonganus* usually restricted to particular islands or groups of islands. *Pteropus ornatus* occurs on the Loyalty Islands and New Caledonia, on the latter island with *P. vetulus* (Felten, 1964c); *P. anetianus*, its several subspecies (Felten, 1964b, Felten & Kock, 1972) and *P. fundatus* occur on the New Hebrides, while *P. tuberculatus*, *P. vanikorensis* and *P. nitendiensis* are found on various of the Santa Cruz Islands. By contrast, the Microchiroptera of these islands and island groups consist chiefly of species with a much wider general distribution, although one, *Miniopterus robustior*, is known only from the Loyalty Islands. Most are Australasian: *Miniopterus australis* and *M. medius* extend to the Loyalty Islands and New Caledonia, *Hipposideros galeritus*, *Aselliscus tricuspidatus*, *Myotis adversus* and *Miniopterus tristis* to the New Hebrides. *Emballonura semicaudata*, widely distributed among the islands of the Pacific to the east, occurs also on the New Hebrides and *Chalinolobus gouldi*, otherwise an Australian species, is represented on New Caledonia (Koopman, 1971 : 4).

The bat species so far recorded from the Fiji Islands are quite clearly consistent with the position of the group in the long island chain that stretches eastward from New Guinea into the Pacific Ocean, the Fiji Islands lying near the eastern limit of bat distribution along the chain and somewhat widely separated from their nearest neighbours to the west. Although four of the five bat species hitherto known from the Fiji Islands occur also on the islands to the west, the absence from the Fijian fauna of the majority of the widespread microchiropteran species that extend eastward to the New Hebrides or even to New Caledonia and the Loyalty Islands suggests that for many the relatively wide oceanic strait between these islands and the Fiji group is an effective barrier to further dispersal. Of bat species found both east and west of this obstacle, only one megachiropteran and one microchiropteran occur further west than New Caledonia and the New Hebrides. Furthermore, differentiation is unusual among Fijian bats, until now there being no endemic species reported from this island group, and but one endemic subspecies. In these circumstances it is of particular interest to report the existence in the Fiji Islands of a hitherto undescribed and very distinct species of the aberrant genus *Pteralopex*, itself previously known only from the Solomon Islands.

## Systematic descriptions

### Genus *PTERALOPEX* Thomas, 1888

*Pteralopex* Thomas, 1888 : 155, 1889 : 473, pl. 20, fig. 3, pl. 21, figs 4–7. *Pteralopex atrata* Thomas, 1888.

The genus *Pteralopex* is characterized externally by the insertion of the wings at or near the mid-line of the back along the spinal line; cranially by an unusually well-developed sagittal crest, long postorbital processes which reach or nearly reach the zygomata, rather upwardly directed orbits and short, broad, nearly parallel-sided rostrum, but especially dentally by massive upper canines which have a prominent posterior supplementary cusp and by the exceptional size of the outer lower incisors ( $i_{2-2}$ )\*. The molariform teeth of *Pteralopex*, moreover, are variously cuspidate, on occasion displaying an extreme of the tendency towards lateral cuspidation seen in various

\* The dental notation adopted in this paper is that of Miller (1907).

ways and to varying degrees in some species of the related genus *Pteropus*, in *Hypsognathus*, *Nyctimene*, *Paranyctimene*, *Dobsonia* or in *Harpyionycteris*, although surface cusps or ridges such as occur in some of *Cynopterus*, in *Ptenochirus*, *Latidens*, *Dyacopterus*, *Thoopterus*, *Dobsonia* or in *Harpyionycteris* are lacking.

The dental formula of *Pteralopex* is  $i \frac{2}{2}, c \frac{1}{1}, pm \frac{3}{3}, m \frac{2}{3} = 34$ , as in *Pteropus*; the upper incisors ( $i^{2-3}$ ) have very broad posterior ledges and the upper canines are short, very thick antero-posteriorly, with a large and prominent posterior secondary cusp extending halfway along the length of the tooth and a wide internal cingulum bearing small internal and postero-internal basal cusps, the anterior cusp sometimes indistinct. The first upper premolar ( $pm^2$ ) is rudimentary, its crown only slightly differentiated; the second ( $pm^3$ ) and third ( $pm^4$ ) upper premolars and the first upper molar ( $m^1$ ) have prominent, shelf-like raised anterior and posterior basal ledges, the labial lateral elevation in these teeth raised into a cuspidate structure, the lingual elevation usually similarly so but on occasion more ridge-like, while the second upper molar ( $m^2$ ) lacks the anterior basal ledge and the cuspidate appearance is usually less evident.

The inner lower incisor ( $i_1$ ) is very small, subterete, its edge slightly lobed, the outer lower incisor ( $i_2$ ) much enlarged to twelve or fifteen times the bulk of  $i_1$ , its posterior ledge very long antero-posteriorly, the longitudinal diameter of the tooth greater than the transverse diameter of its crown, the cutting edge tricuspid or incipiently so. The lower canine is relatively short and stout, its cingulum with generally a small raised postero-external tubercle; the first lower premolar ( $pm_2$ ) subequal in crown area to  $i_2$ , with similar broad inner ledge and tricuspid cutting edge, the central cusp the largest; the second lower premolar ( $pm_3$ ) has a large main cusp, sometimes with a subsidiary anterior cusp, a short posterior basal ledge forming labially a small posterior basal cusp separated from the main cusp by a notch. The third lower premolar ( $pm_4$ ) and the first ( $m_1$ ) and second ( $m_2$ ) lower molars are short and broad, with strong posterior basal ledges more developed lingually than labially and thus oblique, and their lateral elevations are variously cuspidate to differing degrees, the lingual elevation on occasion more ridge-like; third lower molar ( $m_3$ ) usually subcircular, with a concave crushing surface, generally with a shallow notch in its labial margin, but sometimes may be more definitely cuspidate, its crown pattern more nearly similar to that of  $m_2$ .

A comprehensive review of *Pteralopex* as then understood was provided by Andersen (1912 : 432), who had earlier (1909a : 213) studied its affinities in considerable detail. The genus has hitherto included two named forms, *P. atrata* Thomas, 1888 (the type species) and *P. anceps* Andersen, 1909b, the former described from Guadalcanar Island, in the eastern Solomon Islands and later reported (Sanborn, 1931 : 21) from the nearby island of Ysabel, the latter apparently known only from Bougainville Island and from Choiseul Island (Phillips, 1968 : 792), in the more westerly part of the Solomons group. Andersen (1912 : 437) considered the two to be distinct species but Laurie & Hill (1954 : 40) and Phillips (1968 : 790) considered *anceps* a subspecies of *P. atrata*. There is much, however, to commend the original arrangement. The ears of the larger *anceps* have a trace of a blunt tip and although for the most part its pelage is blackish or seal brown, the hairs on the posterior part of the ventral surface are tipped with drab brown. The fur is long and rather woolly, extending to the dorsal surface of the tibia and of the metatarsals, which dorsally are densely haired. In contrast, the ears of *atrata* are more rounded and its pelage uniformly blackish or dark seal brown, rather short and not especially woolly, the fur not extending dorsally to the distal end of the tibia (the last fourth is naked) or to the metatarsals.

Although many dental features such as the enlargement of  $i^{2-3}$  and of  $i_2$ , and the presence of a secondary canine cusp are shared in equal measure by *anceps* and *atrata*, in others there is considerable divergence. In particular, the anterior basal ledges of  $pm^4$  and  $m^1$ , and to a lesser extent of  $pm^3$  are less developed in *anceps* than in *atrata*, and the lingual margins of  $pm_4$ ,  $m_1$  and  $m_2$  are more ridge-like and less cusp-like. According to Andersen (1912 : 437, 438, fig. 22) the anterior basal ledge of  $pm^4$  in *anceps* does not extend internally on to the inner surface of the lingual cusp as it does in *atrata*, but the lingual faces of  $pm^{4-4}$  have been damaged in the subadult holotype and only available specimen of *anceps*, and the observation cannot now be confirmed from this example: according to Phillips (1968 : 792) the anterior basal ledge of  $pm^4$  in adult *anceps*



extends to the labial surface. Certainly the anterior basal ledges of  $pm^3$  and  $m^1$  in *anceps* extend much less obviously on to the inner face of the lingual cusp than in the corresponding teeth of *atrata*. In *anceps* the lingual cusp of  $pm^4$  is long and slightly ridge-like but in *atrata* the corresponding cusp is much more nearly conical: this contrast is more pronounced in  $m_1$  which in *anceps* has a long, ridge-like lingual elevation, scarcely separated from the raised anterior rim of the tooth, but in *atrata* has a prominent, sharply defined antero-internal cusp, or in  $m_2$  where the similarly long, rather low, ridge-like lingual elevation of *anceps* differs from the short, slightly raised corresponding elevation of *atrata*. Furthermore, the labial elevations of  $pm^4$ ,  $m_1$  and  $m_2$  in *anceps* are much less definitely divided into two cusps than in *atrata*, the dividing fissure in  $pm^4$  and  $m_1$  scarcely reaching the labial face of the teeth and barely perceptible in  $m_2$ . In general terms the molariform teeth of *anceps* are nearer in appearance to those of many species of *Pteropus* than are those of *atrata*: the external and dental differences between *anceps* and *atrata* suggest that the two forms must be considered specifically distinct.

### Key to species of *Pteralopex*

- 1 Smaller (length of forearm 116–120 mm); pelage brown overall; labial margin (excluding raised posterior ledge) of  $pm^4$  and  $m^1$  divided into three cusps, the anteriormost very small;  $pm^3$  lacking any lingual cusp; crowns of  $m_1$  and  $m_2$  closely similar . . . . . *P. acrodonta* sp. nov.
- Larger (length of forearm 139–171 mm); pelage predominantly black or blackish seal brown, especially dorsally; labial margin (excluding raised posterior ledge) of  $pm^4$  and  $m^1$  forming a single large cusp;  $pm^3$  with prominent lingual cusp; crowns of  $m_1$  and  $m_2$  dissimilar . . . . . 2
- 2 Smaller (length of forearm 139–144 mm); ventral pelage uniformly black or blackish seal brown; fur short, not especially woolly, extending to entire dorsal surface of tibia and to dorsal surface of metatarsals;  $pm^4$  with subconical lingual cusp; lingual elevations of  $m_1$  and  $m_2$  short, in  $m_1$  forming a sharply defined subconical antero-internal cusp . . . . . *P. atrata*
- Larger (length of forearm 160–171 mm); ventral pelage black or blackish seal brown anteriorly, brownish posteriorly; fur long, woolly, not extending dorsally to distal end of tibia or to dorsal surface of metatarsals;  $pm^4$ ,  $m_1$  and  $m_2$  with lengthened or long ridge-like lingual elevations . . . . . *P. anceps*

### *Pteralopex acrodonta* sp. nov.

**HOLOTYPE.** BM(NH) 77.3097. Adult ♂. Ridge about 300 m NE of the Des Voeux Peak Radio Telephone Antenna Tower, Taveuni Island, Fiji Islands, 16° 50½' S, 179° 58' W, c. 3840 ft (1170 m). Collected 3 May 1977 by W. N. Beckon, died 6–7 May 1977. Caught in mist net on ridge summit: bulldozed land with secondary scrubby growth, adjacent to primary forest. Original number 104. Skin and skull.

**OTHER MATERIAL.** No. 101. Adult ♀. Des Voeux Peak, Taveuni Island, c. 3900 ft (1190 m). Collected 9 November 1976 by W. N. Beckon, died 12 November 1976. Caught in mist net on ridge summit. Skin and skull. To be deposited in the Fiji Museum.

**DIAGNOSIS.** Smaller externally (Table 1) than either *Pteralopex anceps* or *P. atrata*, differing sharply from these in overall brown rather than black or blackish seal brown pelage; skull smaller (Table 1) than in either of the related species, but with relatively wider interorbital region and relatively more massive zygomata which have a more pronounced upward deflection. Teeth, excepting  $m^2$  and  $m_3$ , smaller (Table 2) than in *P. anceps* or *P. atrata*,  $pm^4$ ,  $m^{1-2}$  and  $m_{1-3}$  more cuspidate, (Fig. 1) the labial margin (excluding raised posterior ledge) of  $pm^4$  and  $m^1$  divided into three cusps rather than elevated into a single cusp as in these species;  $m^2$  little reduced, similar in size to  $m^2$  of *P. anceps* or *P. atrata*;  $pm^3$  lacking the prominent internal cusp of  $pm^3$  in *P. anceps* or *P. atrata*, its internal vertical ridge merging smoothly into the tip of the tooth;  $m_1$  and  $m_2$  closely resembling each other, not markedly dissimilar in size and cuspidation as in *P. anceps* and *P. atrata*; crown of  $m_3$  less basin-like than in the related species, its cusp pattern similar to that of  $m_1$  and  $m_2$ .

**DESCRIPTION.** Ears small, short, almost concealed by surrounding fur; upper margin of ear semicircular as in *Pteralopex atrata*, with no indication of any tip; outer surface of conch nearly naked, a few sparse long hairs on its inner surface, clustered a little more thickly near the anterior



Table 1 External and cranial measurements (in millimetres) of *Pteralopex acrodonta*, *P. atrata* and *P. anceps*

	<i>P. acrodonta</i> <sup>1</sup> ♂ BM(NH) Taveuni I., Fiji Is 77.3097	<i>P. acrodonta</i> <sup>1</sup> ♀ No. 101 Taveuni I., Fiji Is	<i>P. atrata</i> <sup>1</sup> ♂ BM(NH) Guadalcanar I.	<i>P. atrata</i> ♂ BM(NH) Guadalcanar I. 89.4.3.3	<i>P. atrata</i> ♀ BM(NH) Guadalcanar I. 89.4.3.1	<i>P. atrata</i> ♀ BM(NH) Guadalcanar I. 34.7.2.31	<i>P. anceps</i> <sup>1, 2</sup> ♀ BM(NH) Bougainville I. 8.11.16.7	<i>P. anceps</i> <sup>1, 2</sup> ♂ <sup>3</sup> Bougainville I. 3	Choiseul I.
Length of forearm	116.5	119.5	141.8	140.5	144.0	139.0	136.3	160-171	
Total length of skull	58.6	57.5	69.9	67.5	65.8	68.0	64.5	77.0-78.9	
Condylbasal length	57.0	56.4	66.6	63.5	63.2	64.7	62.5	73.8-75.5	
Palatal length	32.2	31.8	36.7	36.1	34.7	37.2	34.4		
Length palation to incisive foramina	27.2	26.6	31.2	30.5	29.9	32.3	29.2		
Length front of orbit to tip of nasals	15.7	15.0	18.9	16.9	17.0	19.0	17.2		
Lachrymal width	13.5	13.4	12.8	13.3	13.1	13.3	13.9		
Interorbital width	9.1	9.7	8.8	8.4	8.7	8.9	9.3		
Postorbital width	7.2	8.1	5.4	6.2	6.9	6.6	8.7		
Orbital diameter	12.5	12.4	12.9	13.0	13.1	13.3	12.9		
Zygomatic width	32.5	35.1	38.4	38.0	39.4	39.9	-	42.2-45.4	
Width of braincase	21.5	22.0	22.5	22.7	21.7	23.5	24.8		
Mastoid width	20.6	20.9	22.6	22.3	22.0	23.7	22.5		
c1-c1 (greatest external)	14.2	14.6	17.0	17.2	16.9	15.9	16.7	18.7-21.1	
c1-c1 (external, alveoli)	13.3	13.3	15.2	16.0	15.3	14.4	15.1		
c1-c1 (least internal)	8.0	8.3	9.0	8.9	8.6	8.8	8.3		
pm <sup>4</sup> -pm <sup>4</sup> (least internal)	9.4	9.5	10.6	11.1	11.3	11.1	-		
m <sup>1</sup> -m <sup>1</sup> (external, crowns)	16.0	16.3	20.3	21.6	20.9	20.0	20.5	22.0-25.3	
m <sup>1</sup> -m <sup>1</sup> (external, alveoli)	15.1	15.9	18.5	19.9	19.5	18.5	18.7		
Width of mesopterygoid fossa	6.9	6.6	8.1	9.1	9.1	9.8	8.1	28.2-29.3	
c-m <sup>2</sup>	21.9	22.0 <sup>3</sup>	25.6	26.1	25.4	25.3	25.4		
Length of complete mandible from condyles	44.5	43.3	54.3	53.2	50.2	51.4	48.9		
Length of right ramus from condyle	46.4	45.4	55.8	54.5	52.0	53.6	50.6		
c-m <sub>3</sub>	24.2	24.2	27.8	28.0	27.4	27.4	28.2	31.4-32.8	

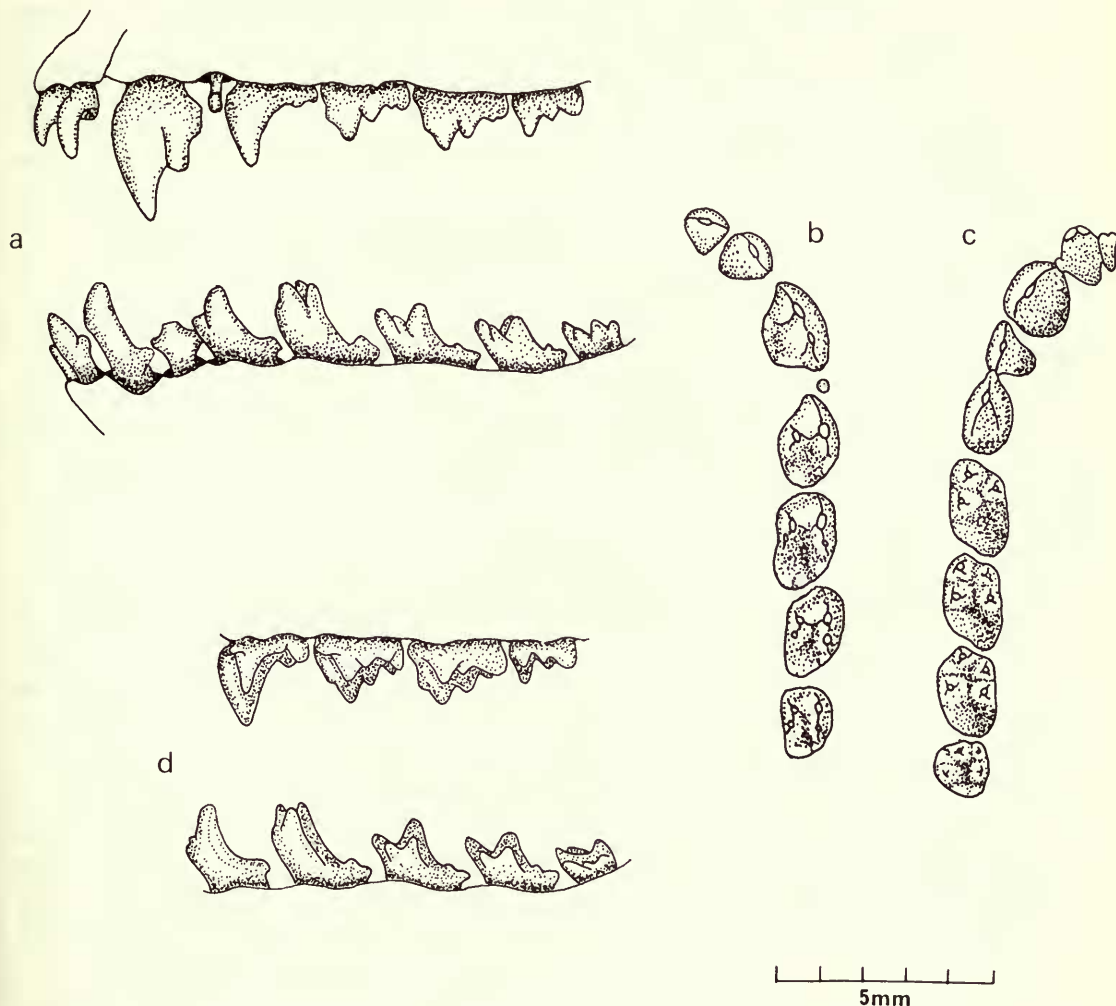
<sup>1</sup> Holotype. <sup>2</sup> Subadult. <sup>3</sup> Left tooththrow. <sup>4</sup> From Phillips (1968: 792)

Table 2 Measurements (in millimetres) of cheekteeth of *Pteralopex acrodonia*, *P. atrata* and *P. anceps*

	<i>P. acrodonia</i> <sup>1</sup> ♂ BM(NH) Taveuni I., Fiji Is 77.3097	<i>P. acrodonia</i> <sup>1</sup> ♀ No. 101 Taveuni I., Fiji Is	<i>P. atrata</i> <sup>1</sup> ♂ BM(NH) Guadalcanar I. 88.1.5.9	<i>P. atrata</i> ♂ BM(NH) Guadalcanar I. 89.4.3.3	<i>P. atrata</i> ♀ BM(NH) Guadalcanar I. 89.4.3.1	<i>P. atrata</i> ♀ BM(NH) Guadalcanar I. 34.7.2.31	<i>P. anceps</i> <sup>1, 2</sup> ♀ BM(NH) Bougainville I. 8.11.16.7
pm <sup>3</sup>							
Length	4.3	4.4	5.1	5.1	5.0	4.5	5.1
Width	3.0	3.1	4.0	4.4	4.2	3.8	4.3
pm <sup>4</sup>							
Length	4.4	4.2	4.9	5.0	5.1	4.6	5.3
Width	3.2	3.2	4.2	4.6	4.2	4.0	-
m <sup>1</sup>							
Length	4.0	3.9	4.5	4.4	4.6	4.0	5.0
Width	2.8	2.8	3.7	3.9	3.8	3.5	4.2
m <sup>2</sup>							
Length	3.6	3.5 <sup>3</sup>	3.2	3.3	3.1	2.7	3.2
Width	2.7	2.6 <sup>3</sup>	2.8	3.0	2.9	2.6	3.0
pm <sub>2</sub>							
Length	2.4	2.4	2.9	3.0	3.0	2.4	3.3
Width	2.4	2.2	3.0	2.9	3.2	2.6	3.2
pm <sub>3</sub>							
Length	4.3	4.3	4.9	4.8	4.8	4.4	5.5
Width	2.3	2.5	3.3	3.6	3.2	3.2	3.3
pm <sub>4</sub>							
Length	4.2	4.1	5.0	5.2	5.1	4.8	5.8
Width	2.6	2.8	3.7	3.9	3.7	3.4	3.7
m <sub>1</sub>							
Length	4.3	4.3	4.5	4.9	4.8	4.5	5.5
Width	2.8	2.8	3.8	3.7	3.6	3.3	3.8
m <sub>2</sub>							
Length	4.1	3.9	3.7	3.7	3.7	3.4	4.0
Width	2.7	2.6	3.4	3.4	3.3	3.1	3.5
m <sub>3</sub>							
Length	2.7	2.3	2.7	2.8	2.7	2.4	2.5
Width	2.4	2.4	2.8	2.7	2.7	2.4	2.7

<sup>1</sup> Holotype. <sup>2</sup> Subadult. <sup>3</sup> Left tooth.

margin of the ear; no antitragal lobe; wings inserted on the back at or near the spinal line, and posteriorly at the base of the first and second toes; second phalange of fourth digit subequal in length to first phalange, not conspicuously longer; uropatagium or interfemoral membrane a very narrow flange; calcar short. Pelage brown overall, dorsally with the hairs mid-brown at the base and for much of their length, over the head, mantle and rump tipped with paler shining brown



**Fig. 1** *Pteralopex acrodonta*. Holotype ♂ BM(NH) 77.3097. a. Labial aspect of left tooththrow. b. Ventral aspect of left upper tooththrow. c. Dorsal aspect of left lower tooththrow. d. Lingual aspect of right molariform teeth.

to give a slightly bronzed appearance, paler hair tips on rump a little less evident than those of mantle; hairs in mid-dorsal region immediately behind mantle bright brown for their entire length, smooth, closely adpressed, forming a longitudinal band about 18–20 mm in width over the innermost part of the wing membranes at their insertion along the mid-line of the body; ventral pelage a drab brown, rather paler than the dorsal pelage, on the lower part of the neck and on the flanks with paler light brown tips. The colour of the new species contrasts sharply with the black coloration of *P. atrata* or with the black dorsal surface of the head and body in *P. anceps*; only in



this latter species the blackish brown colour of the underparts is relieved by drab tipping to the otherwise dark seal brown hairs over the lower part of the chest and over the belly.

Fur long and woolly as in *Pteralopex anceps*; upper surface of forearm thickly clothed with moderately long, adpressed brownish hairs for the proximal two thirds of its length, the hair covering a little more extensive and denser near and at the elbow; tibia densely covered dorsally with thick long hair to the ankle, with a very thin scattering of moderately long, brownish hairs on the upper surface of the phalanges. Dorsal surface of wing and uropatagium or interfemoral membrane largely naked but a narrow band of quite dense, closely adpressed, long bright brown hairs extending along the junction of the mesopatagium with the proximal two thirds of the forearm, around the elbow and across the endopatagium to the rear of the mantle, the median longitudinal mid-dorsal band of long, smoothly adpressed bright brown hairs above the insertion of the endopatagium on the body extending over the proximal part of the membrane; a thin clustering of moderate, blackish brown hairs near the hind margin of the endopatagium at and near its junction with the foot; ventrally a denser band of moderately long brown hairs along the proximal two thirds of the junction of the mesopatagium with the forearm; ventral surface of forearm and tibia with no more than a few very sparse hairs.

*Pteralopex anceps* has a rather dense cover of long black hairs on the proximal third of the dorsal surface of the forearm and the dorsal surface of the tibia is densely clothed with quite long blackish chestnut brown fur, extending to the dorsal surface of the foot over the metatarsals and, more sparsely, to the dorsal surface of the phalanges; there is a band of moderate hairs on the mesopatagium both dorsally and ventrally adjacent to the lower part of the forearm, blackish above, brownish below, but the dorsal band does not extend across the surface of the endopatagium to the rear of the mantle. In *P. atrata* the proximal third of the dorsal surface of the forearm and the dorsal surface of the tibia have only a very sparse cover of moderate black hairs which extend and scatter on to the dorsal surface of the foot over the metatarsals and phalanges; there is no definite band of fur on the dorsal surface of the mesopatagium or of the endopatagium, but the ventral surface of the mesopatagium has a band of brownish hairs along the proximal two thirds of its junction with the forearm.

Skull similar to that of *Pteralopex anceps* or of *P. atrata*, with broad, nearly parallel-sided rostrum, but smaller; sagittal crest well developed but not especially prominent; interorbital region relatively wide; orbits less markedly upwardly directed than in its congeners; zygomata massive, deep, their upper margin forming a strongly pronounced upwardly sweeping curve; nasals terminating anteriorly at a line vertically above the rear of  $i^3$  as in *P. anceps* rather than above the centre of this tooth as in *P. atrata*.

Inner upper incisor ( $i^2$ ) with narrow posterior shelf, less sharply demarcated from the vertical cusp than in *Pteralopex anceps* or *P. atrata*, the junction smoothly curved rather than angular;  $i^3$  with posterior shelf more prominently developed than in  $i^2$  and more sharply demarcated from the vertical cusp, the internal cingulum of the tooth slightly raised as in *P. anceps* and lacking the postero-internal cingulum cusp of  $i^3$  in *P. atrata*. Upper canine very similar to that of *P. anceps* or *P. atrata*, substantial, massively based, its antero-external face shallowly grooved, the principal cusp with sharp anterior and internal ridges and with a large, heavy posterior supporting cusp extending along about two thirds of the length of the tooth, a very small, poorly defined posterior cingulum cusp at its base; a small internal cingulum cusp at and just behind the base of the internal ridge, larger than the corresponding indistinct internal cingulum cusp of *P. anceps* but rather less developed than the corresponding cusp in *P. atrata*, in the unworn dentition followed by two small internal cusplets; postero-internal cingulum cusp small and undeveloped, in contrast to the substantial postero-internal cingulum cusp of the related species, but in these there is little or no trace of any posterior cingulum cusp.

Anterior upper premolar ( $pm^2$ ) small, terete, its circular crown very slightly larger than its shaft;  $pm^3$  with larger labial cusp and smaller lingual cusp as in *Pteralopex anceps* or *P. atrata*, its anterior basal ledge narrower than in those species but nevertheless also extending to the inner face of the tooth, a small basal supplementary postero-external cingulum cusp at rear of main labial cusp;  $pm^4$  strongly cuspidate, labially with a higher central cusp supported by a small anterior subsidiary cusp and a rather more prominent posterior subsidiary cusp, separated from the

posterior basal ledge by a small, undeveloped basal cusp, lingually with a lower but rather more massive cusp supported posteriorly by a small postero-internal basal cusp; anterior and posterior basal ledges well developed, raised, the anterior ledge extending to the inner face of the tooth as in *P. atrata*, the posterior ledge oblique as in *P. anceps*.

First upper molar ( $m^1$ ) very similar to  $pm^4$  with its labial elevation divided into a larger central cusp with smaller anterior and posterior supporting cusps, separated from the raised posterior ledge by a very small basal cusp integral with the ledge and with large lingual cusp, an incipient subsidiary postero-internal cusp at the base of its posterior face;  $m^2$  relatively large, the tooth labially with a large anterior cusp supported posteriorly by a lower subsidiary cusp, the lingual elevation divided into two cusps, the anteriormost much the longer and higher, completely separated anteriorly from the labial elevation by a moderate fissure, the posterior basal ledge well developed, raised and cusp-like. In profile, the labial faces of  $pm^4$  and  $m^1$  present a more or less tricuspid appearance, the anteriormost cusp small and sometimes rudimentary, the second cusp much the largest, supported posteriorly by a well-developed subsidiary cusp, the basal cusp at the rear of this structure barely evident in profile, overshadowed by the large, massive elevated posterior basal ledge. In the same way,  $m^2$  is bicuspid in labial profile, with a large anterior cusp and smaller posterior subsidiary cusp: as in  $pm^4$  and  $m^1$ , the strongly developed, elevated posterior basal ledge appears in profile to be a further posterior cusp. There is a sharp contrast in labial profile between  $pm^4$ ,  $m^1$  and  $m^2$  in *Pteralopex acrodonta* and the corresponding teeth in *P. anceps* and *P. atrata*, which present but a single large cusp, with posteriorly the prominent elevated posterior basal ledge: in *P. atrata* the extreme elevation of this ledge produces the appearance of a posterior cusp, especially in  $m^1$  and  $m^2$ .

Inner lower incisor ( $i_2$ ) as in *Pteralopex anceps* or *P. atrata*, very small, about one twelfth to one fifteenth the bulk of  $i_3$ , its edge slightly widened, faintly and irregularly lobed, its crown triangular in cross-section;  $i_3$  much as in *P. anceps* or *P. atrata*, large, with high, rounded, chisel-like cutting edge, shallowly divided into a small inner and larger central cusp, the latter flanked at its base by a small external basal cusp, and with strong posterior shelf to give the crown a triangular outline; lower canine short and relatively massive, with narrow postero-internal shelf, not differing appreciably from the lower canine in the related species.

First lower premolar ( $pm_2$ ) similar in cross-section to  $i_3$ , as it is in *Pteralopex anceps* or *P. atrata*, but a little smaller than that tooth as in *P. anceps*, its edge with larger central cusp, a rudimentary anterior cusp and a rather more developed posterior cusp;  $pm_3$  faintly bicuspid in labial profile, its large labial cusp with a small anterior subsidiary cusp, the tooth lacking any trace of an internal lingual cusp, its internal ridge integral to the tip, not forming an incipient internal cusp as in *P. anceps* or a well-developed internal cusp as in *P. atrata*, the labial cusp in these species single, with no secondary or subsidiary anterior cusp; posterior basal ledge narrow as in the related species, terminating labially in a small postero-external basal cusp separated from the principal labial cusp by a distinct notch;  $pm_4$  similar to  $pm_4$  of *P. anceps* or *P. atrata*, labially with two well developed cusps, lingually with a single large cusp, the anterior part of the crown divided completely by moderate fissures, the labial cusps divided totally as in *P. atrata*, not partially as in *P. anceps*, the posterior basal ledge broad and oblique as in these species, elevated labially into a postero-external cusp-like structure separated by a distinct notch from the posterior of the larger labial cusps, but undeveloped lingually, as in *P. anceps* and *P. atrata*.

First lower molar ( $m_1$ ) quite different from  $m_1$  in either *Pteralopex anceps* or *P. atrata*, its crown anteriorly elevated as in these species but divided anteriorly by deep longitudinal and transverse fissures into four cusps, two labial and two lingual, the anteriormost labial cusp in the unworn dentition with a slight curving of its postero-external edge which may indicate a further slight degree of cuspidation. The anterior part of the crown thus displays a condition contrasting sharply with *P. anceps* in which the elevated part of the crown of  $m_1$  is only partially divided by shallow fissures and is rather basin-like, the lateral ridges more or less integral with the raised anterior rim, which is divided by a shallow antero-internal groove; the labial ridge has a shallow fissure just extending to its outer face and the lingual ridge is rather long, with a similarly shallow fissure in its internal face. In *P. atrata* the fissures are deeper than in *P. anceps*, creating labially two well-developed cusps and lingually a single large cusp. As in *P. anceps* and *P. atrata*, the



posterior basal ledge of  $m_1$  in *P. acrodonta* is well developed, wide and oblique, elevated labially into a postero-external basal cusp but low lingually, the cusp rather less developed than in the related species.

Second lower molar ( $m_2$ ) closely resembling  $m_1$  but differing in the unworn dentition in having the labial elevation divided into three cusps, the large anterior labial cusp having a small subsidiary cusp shallowly divided from its postero-external face, the whole deeply separated from a more posteriorly placed large labial cusp, the two anterior cusps eroding with wear to a single, large flattened structure. The anterior part of the crown differs widely from the corresponding part of the crown of  $m_2$  in *Pteralopex anceps* from which cusps are effectively lacking, the labial ridge only faintly divided and then incompletely, the lingual ridge long and undivided, both ridges integral with the raised anterior margin to form an elevated rim round much of the anterior part of the tooth. The anterior part of the crown of  $m_2$  in *P. atrata* is similar to that of *P. anceps*, but the labial ridge is very shallowly divided by a slight fissure and the lingual ridge is relatively shorter and slightly cusp-like, faintly divided from the raised anterior margin. The posterior basal ledge of  $m_2$  in *P. acrodonta* resembles that of  $m_1$  and is similarly well developed, wide and oblique, elevated labially into a low basal cusp. In *P. anceps* the posterior basal ledge of  $m_2$  is much developed postero-externally into a large cusp-like structure not clearly separated from the labial ridge but is similarly low lingually, while in *P. atrata* the ledge is elevated postero-externally into a distinct large cusp, separated from the main labial ridge by a deep notch. In *P. anceps*, therefore, the crown of  $m_2$  is basin-like, its central depression opening postero-internally but otherwise surrounded by elevated ridges: in *P. atrata* shallow fissures appear in the anterior and labial of these ridges, the lingual ridge is shorter and more cusp-like and the labial ridge is quite clearly separated from the small cusp that forms the labial termination of the posterior basal ledge. In *P. acrodonta* the basin-like pattern is absent, the tooth with a group of elevated cusps anteriorly and a broad, low posterior basal ledge that is only slightly elevated labially.

Third lower molar ( $m_3$ ) relatively large, similar in size to  $m_3$  in *Pteralopex anceps* or *P. atrata*, the anterior cusp pattern in the unworn dentition similar to that of  $m_2$ , with three labial and two lingual cusps, the anterior labial cusp large, with a small subsidiary cusp shallowly divided from its postero-external face, deeply separated from a more posteriorly situated large posterior labial cusp, and much of the crown of the tooth traversed by relatively deep longitudinal and transverse fissures; posterior basal ledge narrow and short, elevated, shallowly divided into two small unequal basal cusps, the outer smaller, the inner rather larger. The cusp pattern is greatly eroded in the worn dentition to produce two flattened cusps anteriorly, one labial, one lingual, separated by a shallow longitudinal fissure, both separated by a deeper transverse fissure from the low, cusp-like remnants of the posterior labial and lingual cusps and of the raised posterior basal ledge. The crown of  $m_3$  in *P. acrodonta* contrasts sharply with that of  $m_3$  in *P. anceps* in which no cusps are evident and which has instead very short lateral ridges, contiguous with the raised anterior margin, the posterior margin greatly developed and elevated, separated from the labial ridge by a shallow notch, the central depressed area of the tooth opening postero-internally as in  $m_2$  of that species. There are similar contrasts with the crown of  $m_3$  in *P. atrata*, which has very similar short lateral ridges, the lingual ridge slightly cusp-like, separated from the raised anterior margin by a faint indentation, the posterior margin elevated labially into a rounded cusp, separated from the labial ridge by a shallow notch, and the central area of the tooth opening postero-internally as in *P. anceps*.

The anterior parts of  $pm_4$  and  $m_1$  in *Pteralopex acrodonta* are strongly bicuspid in labial profile, with  $m_2$  and  $m_3$  more or less tricuspid in the unworn dentition when the large anterior cusp and its associated subsidiary cusp are clearly defined, but bicuspid when wear has occurred. The small external basal cusp terminating the posterior basal ledge in  $pm_4$ ,  $m_1$  and  $m_2$  suggests an additional, low posterior cusp behind the main elevation. The lower molariform teeth of *P. acrodonta* differ sharply in profile from those of *P. anceps* in which only a slight indication of a division of the labial ridge into two cusps can be seen in  $pm_4$  and  $m_1$ , is imperceptible in  $m_2$  and absent from  $m_3$ . In labial profile they more nearly resemble the lower molariform teeth in *P. atrata* where the labial ridge in  $pm_4$  and  $m_1$  is clearly bicuspid, that of  $m_2$  faintly so but  $m_3$  lacks any division of the labial ridge. The lingual profile of  $pm_4$  is similar in the three species, but *P. acrodonta* differs



markedly from *P. anceps* and *P. atrata* in the lingual profile of  $m_1$  and  $m_2$ . The lingual elevation of these teeth in *P. acrodonta*, although long, is deeply divided into two cusps but in *P. anceps* presents an uninterrupted ridge-like lingual elevation which is shorter and raised into a single large cusp in *P. atrata*. The lingual profile of  $m_3$  differs similarly. In the unworn dentition of *P. acrodonta* its lingual elevation is bicuspid although in the worn dentition the posterior cusp tends to erode into the posterior basal ledge: in *P. anceps* there is a low lingual ridge which in *P. atrata* is anteriorly higher and a little more cusp-like.

**ETYMOLOGY.** The specific name is derived from *ἄκρος*, pointed, and *ὀδών* = *ὀδούς*, tooth, in allusion to the many pointed summits of the molariform teeth in the new species.

**BIOLOGY.** Little is known of the biology of this species: the male was not reproductively active when captured, and the female not pregnant.

**REMARKS.** This interesting new species was discovered by the junior author and his wife, who obtained a single example on Taveuni in the latter part of 1976. They visited the island again in 1977 when two more specimens were caught, one of which escaped. It is possible that the species may be the 'white' fruit bat described by Mr Vasu Shankaran, an Indian resident of Taveuni, and known as the 'beka lulu' by the local population. This 'white' bat was reported in the lower forest of the Nasinu area, about 13½ km SSW of Waiyevo, but while camped there no specimens were netted although many bats were seen circling in the forest during the early evening. Mr Shankaran remarked that this bat usually roosted in pairs in the fern clumps growing some 6–10 m from the ground on the trunks of the larger trees in the open, tall forest, leaving the clump when disturbed but flying only a short distance before landing again, unlike the other Fijian fruit bats which are more colonial and which desert their roost when an intruder approaches. This observation is supported by Mr Robin Mercer, a planter and naturalist of Savusavu in Vanua Levu, who said that the Fijians of that island use the term 'beka lulu' for a light coloured fruit bat that circles the roost instead of flying away when disturbed: he had thought such bats to be old, hoary individuals of the known species. A different pattern of erratic, manoeuvring flight, suggesting the hunting of insects, was noted in large bats over Des Voeux Peak on Taveuni. The name 'beka lulu' or 'mbeka lulu' appears in a list of Fijian names (Macdonald, 1857 : 267) collected during an expedition up the Rewa River and its tributaries in 1856 and also in the New Fijian Dictionary of Capell (1973) where it is defined as a 'species of bat'. The term apparently refers to its reputed owl-like colour and large eyes: in life the eyes of *Pteralopex acrodonta*, although not unusually large, are bright orange and very conspicuous. From the pattern of bird distribution in the Fiji Islands, too, it seems possible that in due course the species will be found in Vanua Levu, across the narrow Somosomo Strait from Taveuni Island.

### Relationships

Andersen (1909a : 218) discussed the diagnostic characters and affinities of *Pteralopex* in detail and concluded that it was closely related to the *pselaphon* group of *Pteropus* (including *P. insularis*, *P. phaeocephalus*, *P. pselaphon*, *P. pilosus*, *P. tuberculatus* and *P. leucopterus*), some members of this group displaying to a greater or lesser extent many of those features that appear in more exaggerated form in *Pteralopex anceps* or in *P. atrata*. The newly described species adds support to this opinion. The distribution of the fur, the shape of the skull, its long postorbital processes that do not reach the zygomata, the lack of postorbital zygomatic processes, its short, broad rostrum, heavy premaxillae and its high, broad coronoid rising at about a right angle from the horizontal ramus, with broad, steeply sloping gonys are all features of *Pteralopex* that are foreshadowed in the *pselaphon* group of *Pteropus*. The dentition of *Pteralopex acrodonta*, although more extreme and further removed from that of *Pteropus* than the dental structure either of *Pteralopex anceps* or of *P. atrata*, has nevertheless a number of interesting features that extend the parallels drawn by Andersen between the dental architecture of *Pteralopex* and that of the members of the *pselaphon* group of *Pteropus*, especially of *P. pselaphon*, *P. pilosus*, *P. tuberculatus* and *P. leucopterus*.

The posterior shelf of  $i^2$  is narrower in *Pteralopex acrodonta* than in *P. anceps* or *P. atrata* and is slightly less sharply demarcated from the vertical cusp, with a smooth, more rounded transitional area rather than a right-angled junction such as occurs in these species, and  $i^3$  is relatively smaller than in *P. anceps* or *P. atrata*, about one and one half times greater in bulk than  $i^2$  rather than two times or more its bulk as in the other species of *Pteralopex*. In these features  $i^{2-3}$  of *Pteralopex acrodonta* resemble those of the members of the *Pteropus pselaphon* group and, indeed, approach the condition found in *P. leucopterus*. The upper canine in *Pteralopex acrodonta* resembles the upper canine of *P. anceps* or *P. atrata* in the structure of the principal cusp and its major subsidiary cusp, but the postero-internal basal cingulum cusp is smaller and lower than in these species. In the *Pteropus pselaphon* group internal cingulum cusps at the base of the canine are when present usually low and irregular, except in *P. pilosus* which has a large postero-internal basal cusp and a smaller internal basal cusp. The lower incisors and lower canines of the new species are characteristically those of *Pteralopex*.

Certain features of the post-canine dentition of *Pteralopex acrodonta* also find a precedent among the members of the *pselaphon* group of *Pteropus*. The second lower premolar ( $pm_3$ ) in lacking any well-defined internal cusp in *Pteralopex acrodonta* differs sharply from  $pm_3$  in *P. anceps* and *P. atrata*: in the *Pteropus pselaphon* group, *P. pselaphon*, *P. pilosus* and *P. tuberculatus* have an internal shoulder on  $pm_3$  that clearly represents such a cusp but in *P. leucopterus* the internal ridge of  $pm_3$  merges smoothly into the summit of the tooth, as in the new species. The third lower premolar ( $pm_4$ ) and  $m_{1-2}$  are also of especial interest in *Pteralopex acrodonta*. In this species, as in *Pteralopex anceps* and *P. atrata*, these teeth are short and broad with oblique, labially more developed posterior ledge, but while  $pm_4$  in *P. acrodonta* is otherwise very similar to  $pm_4$  of *P. anceps* and more especially of *P. atrata*, the lingual elevation of  $m_1$  and  $m_2$  (and also of  $m_3$ ) is divided into two cusps in contrast to the undivided lingual ridge of  $m_1$  and  $m_2$  in these species. As Andersen (1909 : 221) pointed out, in the *Pteropus pselaphon* group it is the inner or lingual ridge of  $pm_4$  and  $m_1$  that is divided in *P. pselaphon*, while in *P. leucopterus* the inner ridge of  $m_1$  and  $m_2$  is faintly divided, with a lesser or scarcely perceptible division in the outer or labial ridge of the same teeth. This author commented that in *Pteralopex*, as it was then understood, there was a further development of a tendency already apparent in the *Pteropus pselaphon* group but that division had shifted, so to say, from the inner or lingual elevation to the outer or labial elevation (there is in fact a shallow internal fissure in the internal face of the inner ridge of  $m_1$  in *Pteralopex anceps* that does not extend to the edge of the tooth), but in *P. acrodonta* the cuspid condition appears very strongly in both the lingual and the labial elevations of  $m_1$  and  $m_2$ . The crowns of these teeth in *P. acrodonta* present a multicuspid appearance that finds a weak parallel in *Pteropus leucopterus*, albeit very much less strongly emphasized. Furthermore, in *Pteralopex acrodonta* the much increased degree of cuspidation extends to  $m^2$  and  $m_3$ , which are less reduced than in *P. anceps* or *P. atrata*, with  $m^2$  at least three quarters rather than about one half or less the size of  $m^1$  and larger than the corresponding tooth in the related species, and  $m_3$  one half rather than one third the size of  $m_2$ , about the same size as  $m_3$  of *P. anceps* or *P. atrata*. These features suggest a tendency to obtain a maximum of occlusal area in the teeth, despite the smaller size of the newly described bat when compared with its congeners. The geographical distribution of the dental characters among the three species of *Pteralopex* is also of interest. The least cuspidate molariform dentition, most like that of *Pteropus*, is to be found in the westernmost species, *P. anceps*. The most cuspidate dentition, least like that of *Pteropus*, is found in the easternmost species, *P. acrodonta*. A condition intermediate between these extremes occurs in the geographically central species, *P. atrata*.

### Dental homologies and dental evolution

The larger of the pteropodid post-canine teeth have generally a rather characteristic appearance, consisting basically of a rectangular or more or less square crown, with a large labial and a small lingual elevation: these elevations are higher and more developed on the anterior teeth and less so in those that lie towards the rear of the toothrows, particularly in the last lower molar where they may be little more than longitudinal ridges along each side of the tooth. The elevations are



higher in the anterior part of each tooth, with an oblique crushing surface, and lower in the posterior part, the crushing surface more nearly flat. The median division between the two elevations in the first of the larger teeth in each jaw is either obscured by a high, ridge-like commissure, or, often, they merge to form a single large cusp.

Miller (1907 : 41) suggested that it may be assumed (from analogy with the fruit-eating phyllostomatids) that in the upper molars the labial of these elevations is the paracone, the lingual elevation the protocone, while in the lower molars the labial elevation is the protoconid, its lingual counterpart the metaconid. More recently, Slaughter (1970 : 77) considered further that in the upper molars the metacone has been incorporated into the labial ridge and the hypocone into the lingual ridge, while the ridges of the lower molars similarly incorporate the hypoconid labially and the entoconid lingually. Additional small subsidiary cusps are present in several of the Pteropodidae, reaching an extreme in *Harpyionycteris* and *Pteralopex* but also present to some degree in *Hypsignathus*, *Dobsonia*, *Cynopterus*, *Ptenochirus*, *Dyacopterus*, *Thoopterus*, *Nyctimene* and *Paranyctimene*, while some division of the lateral ridges is apparent in a few species of *Pteropus*. The view adopted by Slaughter (p. 56, figs 1I, 1H, p. 77) is that the small subsidiary cusp on the posterior slope of the main labial cusp of the upper molariform teeth of *Dobsonia*, *Nyctimene* and sometimes *Cynopterus* is a rudimentary metacone and that likewise the small subsidiary cusp on the posterior slope of the principal labial cusp of the corresponding lower teeth is a rudimentary protostylid. On this basis Slaughter suggests or infers (p. 56, fig. 1H, p. 78) that in *Harpyionycteris* the last upper premolar (pm<sup>4</sup>) consists labially of the paracone and metacone, lingually the protocone, pm<sub>4</sub> consisting of a tall protoconid flanked postero-labially by a well-developed protostylid, and lingually by a prominent metastylid, there being no metaconid. According to this author, the upper molars in *Harpyionycteris* retain the paracone and protocone, the metacone lying behind the paracone, and on occasion supporting a posterior metastyle. Lingually, the posteriormost cusp is the hypocone. The lower molars have anteriorly the protoconid and metaconid, the labial protoconid followed by a protostylid, the lingual metaconid by a metastylid: the third labial cusp is a small hypoconid, the third lingual cusp the entoconid, the stylids being as well developed as the other cusps.

Support for such close homology between the multiple cusps of the molariform teeth in certain of the Megachiroptera and the cusps of the Microchiroptera dentition is lacking or contradictory. Convincing palaeontological evidence has yet to be found: such cusps in the Megachiroptera occur sporadically, antero-internally, postero-externally, laterally, or on the crown of the tooth, sometimes as a short, raised ridge. In one form or another, or in combination, they are to be found in varying degrees in several of the megachiropteran genera. Even within the species their occurrence is irregular and variable: Peterson & Fenton (1970 : 5) have pointed out that in eight examples of *Harpyionycteris whiteheadi* no two specimens can be said to be even close to identical in the cusp pattern of m<sup>1</sup> and m<sup>2</sup>. In this series the cusps vary in size, position and number, with the addition of accessory cusps to the basic pattern, or with the division of primary cusps into two elements, even between the corresponding right and left teeth of individuals, to the extent that these authors considered the variability of cusp patterns in *Harpyionycteris* to be unique among bats and certainly ranking high among mammals. It is difficult to avoid the conclusion that such multiple cusps cannot be properly homologized with the cusps of the Microchiroptera.

Thomas (1889 : 473), although admitting in an expanded description of *Pteralopex* that it might be thought at first sight that the genus was a highly specialized offshoot of *Pteropus*, considered that its cuspidate teeth most probably represented a survival from the cuspidate dentition that the ancestors of the Pteropodidae might be presumed to have possessed, largely on account of the 'tuberculo-sectorial' appearance of the third premolar and first molar. Later, Thomas (1896 : 243, 1898 : 384) also suggested that the cuspidate canines of *Harpyionycteris* might also owe their origin to a presumably cuspidate-toothed condition among the ancestors of the Pteropodidae. Miller (1907 : 41), although suggesting homology between the anterior of the molar cusps of the Pteropodidae and the protocone, paracone, protoconid and metaconid of the microchiropteran tooth, considered that additional cusps and ridges were not homologous and noted that the tendency to produce supernumerary cusps reached its extreme in *Pteralopex* and *Harpyionycteris*. A similar view was adopted by Andersen (1909a : 222; 1912 : xxix, 435)



who considered *Pteralopex* to be a very specialized offshoot of *Pteropus*, more particularly of the *Pteropus pselaphon* group, the dental peculiarities of *Pteralopex* deriving in his opinion directly from tendencies already latent in the members of that group. Winge (1923 : 263; 1941 : 305) was also unable to recognize the tooth structure of the insectivorous bats in the multicuspidate cheek-teeth of *Pteralopex* and, indeed, found nothing else in its dentition to indicate primitive conditions, repeating the opinions of Miller and Andersen that *Pteralopex* is a highly modified pteropodid. Similarly, Tate (1951 : 4), in considering the dentition of *Harpyionycteris* in relation to the megachiropteran assemblage as a whole, suspected that its multicuspid molars, and the entire dentition, must be regarded as secondary rather than as a surviving example that represented a formerly widespread condition in the Megachiroptera. However, Phillips (1968 : 790) thought Thomas probably correct in considering *Pteralopex* to be an isolated relic.

Slaughter (1970 : 51) has examined possible evolutionary trends in the dentition of the Chiroptera. In discussing the Megachiroptera, this author (p. 77) reviewed the features reported for the fragmentary dentition of reputedly the earliest known megachiropteran, *Archaeopteropus transiens* Meschinelli, 1903, from the Oligocene of Italy, and concluded that only *Harpyionycteris* among living genera had a cuspidate molariform dentition that in any way approached the dentition ascribed to *Archaeopteropus*. However, little is known of the true nature of the ancestral dentition of the Megachiroptera, and Smith (1976 : 53) has remarked that there is apparently no dentition remotely similar to the 'primitive' dilambdodont condition among either the living or the fossil megachiropterans. The argument for megachiropteran dental evolution that Slaughter based on a supposed similarity between the dentitions of *Archaeopteropus* and *Harpyionycteris* was thought by Smith to be weak.

In developing his theme, Slaughter (1970 : 78) considered that the dentition of *Pteralopex* indicated that emphasis shifted very early from a cuspid state to one of U-shaped lophs, minimal dental erosion exposing a rodent-like pattern of dentine. Thus, in *Pteralopex*, the crown of a partially worn upper molar will present (Slaughter, p. 65, fig. 3H) a U-shaped fossette, opening labially, the lower molars presenting two similar lophs or fossettes, the anterior opening to the rear, the posterior opening forward. He considered that the origin of the dental patterns of *Pteralopex* could be easily understood by comparison with *Harpyionycteris* and, indeed, would derive the dentition of *Pteralopex* from that of a *Harpyionycteris*-like form. This presumed loph pattern is not entirely supported by the specimens examined in the course of the present study. In *Pteralopex anceps*  $m^1$  and  $m^2$  have clearly a labially opening fossette, but occasionally in *P. atrata* the high, anterior cusp-like part of each tooth is divided lingually from the elevated posterior basal ledge (hypocone and metastylar cusp of Slaughter) as deeply or almost as deeply as it is labially so that wear will expose an anterior and a posterior loph, rather than a U-shaped rim, or the fossette so formed may be rimmed lingually by a low, narrow unworn ridge rather than the broad ridge figured by Slaughter. The lingual ridge of  $pm^4$  in *P. atrata* may also rarely be similarly deeply divided from the posterior basal ledge. The upper molariform dentition of *P. acrodonta* differs quite sharply from the concept of labially opening fossettes: the lingual division between the anterior part of the tooth and the posterior basal ledge in  $pm^4$ ,  $m^1$  and  $m^2$  is deeper than the labial division so that the fossette opens lingually rather than labially, but with a depression in the postero-external part of its labial rim.

In the mandible, the anterior cusps of  $m_1$ ,  $m_2$  and  $m_3$  in *Pteralopex anceps*, *P. atrata* and *P. acrodonta* provide the necessary basis for the posteriorly directed, U-shaped anterior loph postulated by Slaughter but it is more difficult to establish a foundation for a similar but anteriorly directed posterior loph in the specimens examined. There is little trace of such a loph in  $m_1$  of any of these species: in this tooth the posterior basal ridge consists of little more than a low labial postero-external cusp, with no lingual elevation, the postero-internal part of the tooth flattened, the internal fossette thus opening postero-lingually. The posterior part of  $m_2$  in *P. atrata* and *P. acrodonta* is similar to the corresponding area of  $m_1$ , except that in *P. atrata* the posterior basal ridge and its postero-external cusp is larger and more massive: in both species the crown is low and flat postero-internally, as in  $m_1$ , the posterior basal ridge extending rather more than half-way across the rear of the tooth, the internal fossette opening postero-lingually. In *P. anceps* the posterior basal ridge of  $m_2$  has a very large postero-external cusp forming an internal part of the

labial ridge, and extends across the rear of the tooth almost to its internal corner. Thus with wear the crown of the tooth will become more basin-like, its central fossette opening postero-lingually on to a small, flattened area. Posteriorly,  $m_3$  in *P. atrata* is broadly similar to  $m_2$  but the posterior basal ridge is a little heavier and extends a little further across the tooth, the internal fossette opening postero-lingually. In *P. anceps* the posterior basal ridge of  $m_3$  is heavy, more or less integral with the labial ridge and extending to the inner corner of the tooth, much as in  $m_2$ , the fossette opening lingually, while in *P. acrodonta* the posterior basal ridge of  $m_3$  although a little elevated is narrow and short and can scarcely enclose any internal fossette.

The suggestion that the dentition of *Pteralopex* might derive from a *Harpyionycteris*-like form also deserves close examination, especially since the extremely cuspidate molariform teeth of *Pteralopex acrodonta* have a number of similarities with the corresponding teeth in *Harpyionycteris*. They do, however, differ from the molariform teeth of *Harpyionycteris* in several features. The last upper premolar ( $pm^4$ ) in *P. acrodonta* closely resembles its counterpart in *Harpyionycteris*, its major labial cusp with a small posterior subsidiary cusp as in that genus, but has additionally a smaller anterior cusp, not evident in *Harpyionycteris*, while the lingual cusp has small anterior and posterior basal cusps which are barely if at all evident in that genus. The anterior basal ledge of the tooth is a little wider and flatter in *P. acrodonta*, and the posterior basal ledge larger and heavier, not clearly divided into two cusps as in *Harpyionycteris*. The upper molars ( $m^{1-2}$ ) of *P. acrodonta*, although basically with the same cusp pattern as those of *Harpyionycteris*, have more elevated crowns, with the cusps less clearly divided: the main labial cusp of  $m^1$  has an additional rudimentary subsidiary cusp on its anterior face and in both teeth the anterior basal ledge is more developed, the posterior basal ledge more elevated, heavier and more massive, not divided into two cusps. In *Harpyionycteris* the posterior basal ledge in  $m^1$  is divided into two cusps but in  $m^2$  it forms an indistinctly divided postero-internal cusp: accessory cusps are sometimes present in these teeth (Peterson & Fenton, 1970 : 7, fig. 2) but usually lingually. As in *P. acrodonta*,  $m^2$  is relatively unreduced.

The lower molariform dentitions of *Pteralopex acrodonta* and *Harpyionycteris* have similar resemblances and differences. The principal cusps of  $pm_4$  in both form an anterior 'trigonid', but in *Harpyionycteris* the tooth has additionally an anterior basal cusp and there is a small subsidiary cusp on the posterior face of the principal lingual cusp. The first lower molar ( $m_1$ ) of *P. acrodonta* has anteriorly a group of four well-divided cusps arranged laterally in two pairs, the antero-labial of these with perhaps a faint trace of further cuspidation. Posteriorly, the tooth has a small low external basal cusp and its internal part is low and flattened. This configuration resembles the crown of  $m_1$  in *Harpyionycteris* except that in this genus the anterior part of the tooth has three rather than two lingual cusps. The second lower molar ( $m_2$ ) in *P. acrodonta* is similar to  $m_1$ , with the anterior part of the crown clearly divided, but in the unworn dentition the large antero-labial cusp has a smaller subsidiary cusp divided from its postero-external face, so that effectively there are three labial cusps: lingually,  $m_2$  in *P. acrodonta* has two cusps, as in  $m_1$ . Posteriorly, there is a low external basal cusp flanking the low, flattened internal part of the tooth. In contrast, the anterior part of  $m_2$  in *Harpyionycteris* has two labial and three lingual cusps: posteriorly, the tooth resembles  $m_2$  of *P. acrodonta*. The unworn cuspidation of the anterior part of  $m_3$  in *P. acrodonta* is similar to that of the anterior part of  $m_2$ , with a group of three labial and two lingual cusps, the first two labially consisting of a larger cusp with a smaller subsidiary cusp divided from its postero-external face. Posteriorly, however, the tooth is strongly elevated and slightly cuspidate, its internal part not low and flattened. In *Harpyionycteris* the anterior part of  $m_3$  has two labial and three lingual cusps: posteriorly, there is a low external basal cusp but the internal part of the tooth is low and flattened as it is in  $m_2$ . However,  $m_3$  in *Harpyionycteris* is relatively unreduced, in this respect resembling  $m_3$  in *P. acrodonta*.

It is clear, therefore, that *Pteralopex acrodonta* resembles *Harpyionycteris* quite closely in the major details of its molariform teeth, differing chiefly in a slightly greater degree of development of the basal ledges of  $pm^4$ ,  $m^1$  and  $m^2$ , in the greater elevation of the crowns of the latter two teeth, and in certain details of cuspidation. The degree and pattern of cuspidation, especially where accessory cusps are concerned, may prove variable to some extent: only the holotype of *H. whiteheadi whiteheadi* has been available for comparison but variability in the cusps of  $m^1$  and  $m^2$



in *H. w. negrosensis* has been clearly demonstrated by Peterson & Fenton (1970 : 5, 7, fig. 2). In other respects the dentition of *Harpyionycteris* differs widely from that of *P. acrodonta*, as in its reduced number of incisors with the specialized structure and proclivity of the upper pair, this latter a character shared with the upper canines, and the effective obsolescence of lower incisors with their apparent substitution by strongly tricuspidate, rather incisiform, slightly procumbent lower canines, supplemented by well-developed anterior lower premolars ( $pm_{2-2}$ ). These extensive differences militate against the view that the dentition of *Pteralopex* can be derived from a *Harpyionycteris*-like form: Andersen (1909a : 220) considered that the structure of  $pm^3$ ,  $pm^4$  and  $m^1$  in *Pteralopex* could be derived very easily from that of the corresponding teeth of any species of *Pteropus* and had most probably originated from teeth in which the posterior basal ledge was already more than usually developed, as for instance in the members of the *pselaphon* group of *Pteropus* or in *Pteropus samoensis*; in the *P. pselaphon* group the anterior cingulum of  $pm^3$  and  $pm^4$  is also raised. Furthermore, this author (pp. 217, 220) presented a detailed case for the progressive division of the lateral ridges of certain of the lower molariform teeth in *Pteropus*. In the majority of species the ridges are simple: in *P. samoensis* and *P. pilosus* a faint depression in the inner or lingual ridge of  $pm_4$  suggested an initial division to Andersen, leading to *P. pselaphon* in which the inner ridges of  $pm_4$  and  $m_1$  are very distinctly divided and to *P. leucopterus* in which there is a depression in the inner ridges of  $m_1$  and  $m_2$ , with usually a shallower depression in the outer or labial ridges of these teeth, although it may sometimes be absent or scarcely detectable. This same process can be discerned more vividly in the three species of *Pteralopex*, from a least emphatic, *Pteropus*-like condition in *Pteralopex anceps*, approaching the *pselaphon* group of *Pteropus* as exemplified by *P. pilosus*, *P. pselaphon* and *P. leucopterus*, through an intermediate stage in *Pteralopex atrata*, to the strongly multicuspidate condition of *P. acrodonta*.

The hypothesis that the multicuspidate molariform teeth of *Pteralopex* are an extreme in the Pteropodine dentition is attractive: an opposite extreme is to be found in the low, broadened and rounded cusps and ridges of the molariform teeth of *Styloctenium* or of *Aproteles* Menzies, 1977. Although Andersen (1909a : 220) suggested that the multicuspidate condition could be derived from the molariform dentition of *Pteropus*, it is perhaps more plausible to suggest that the smoother or laterally ridged crown represents a derived condition, the cuspidate crown a less modified state. The links between the dentition of *Pteralopex* and the *pselaphon* group of *Pteropus*, rather than indicating *Pteralopex* to be a specialized offshoot of *Pteropus* as Anderson (1909a : 222) thought at one time, may well indicate that *Pteralopex* and the *Pteropus pselaphon* group derive from a close common ancestor. Andersen (1912 : l) himself later adopted a similar view, considering it scarcely open to doubt that *Pteralopex* had developed from a bat closely related to the living species of the *Pteropus pselaphon* group, or, in other words, that the genus (as it was then understood) was a peculiarly modified representative of that group in the Solomon Islands.

The adaptive significance of the multicuspidate dentition in *Harpyionycteris* was discussed briefly by Peterson & Fenton (1970 : 7) who speculated that, like most of its allies, *Harpyionycteris* is a fruit eater, perhaps adapted for a particular type of tough-textured fruit, the multicuspidate teeth being valuable in extracting the juice. Similar considerations may apply to *Pteralopex* (Sanborn, (1931 : 21) reported *P. atrata* feeding on green coconuts) and especially to *P. acrodonta* which closely resembles *Harpyionycteris* in the extent of cuspidation and in the lack of reduction of the last molars, both adaptations that apparently maintain a maximum of occlusal area despite relatively small overall size. *Harpyionycteris* is rather isolated within the Pteropodidae, having been given subfamilial status by Miller (1907 : 77) and by Andersen (1912 : 799), who, however, remarked (p. 803) that but for the fact that the plan of his Catalogue of 1912 had been predetermined before detailed work had been undertaken the genus ought to have been classed in the Pteropodinae, immediately after *Dobsonia*. Tate (1951 : 4) doubted the association with *Dobsonia* (this author misinterpreted Andersen's action in according subfamilial rank to *Harpyionycteris* as a lack of conviction in his association of the genus with *Dobsonia*) and suggested a connection with *Nyctimene*. Koopman & Cockrum (1967 : 116) also accorded subfamilial rank to *Harpyionycteris* but more recently Koopman & Jones (1970 : 23) preferred tribal status for the genus, within the Pteropodinae. On the other hand, Schultz (1970) noted its isolated systematic position in the Megachiroptera and considered that its multicuspidate molars indicated that it did not live



exclusively on fruit. He concluded that certain morphological features of the digestive tract (notably the structure of the intestinal mucosa) pointed to an early separation from other pteropodids, and consequently postulated familial rank as the Harpyionycteridae. Hitherto among the Megachiroptera, extreme cuspidation of the molariform teeth has been unique and diagnostic to *Harpyionycteris* and for any higher category based upon it. In contrast, the multicuspidate condition in *Pteralopex acrodonta* can be linked through *P. atrata* and *P. anceps* to the condition more general among the other members of the Pteropodinae.

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